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LIFE HISTORY TRADE-OFFS DURING THE SEED-TO-SEEDLING TRANSITION IN A SUBTROPICAL WET FOREST COMMUNITY

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Running head: Seed to seedling transition in Puerto Rico

SUMMARY

1. The transition from seed to established seedling (STS) represents a major bottleneck in plant demography with implications for community dynamics and the maintenance of species diversity. The relative strength of seed limitation versus seedling establishment limitation can reveal life history trade-offs that contribute to the maintenance of community diversity. If seed limitation dominates, chance arrival to open sites may play a key role in maintaining diversity. If seedling establishment limitation dominates, however, species relative abundances may depend more on tolerance to environmental and biotic conditions during seedling establishment (*i.e.* species-specific regeneration niche).

2. We used 3 years of seed rain and seedling recruitment data for 19 species of tropical woody plants collected in the Luquillo Forest Dynamics Plot in Puerto Rico to (i) examine a trade-off between seed and seedling establishment limitation, and (ii) quantify the biotic and abiotic factors that mediate the STS transition.

3. We did not find evidence of a life-history trade-off in the form of a negative correlation between seed and seedling establishment limitation. However, species varied considerably in the relative levels of seed and seedling establishment limitation they displayed. Seed mass correlated negatively with seedling establishment limitation but not with seed limitation. We found striking differences in STS transition between life forms categorized as trees (including two palms) and lianas; lianas exhibited significantly higher STS transition rates than trees.

4. The biotic and abiotic variables most strongly associated with successful STS transition differed between life forms. For trees, conspecific seed density and temporal

fruiting concentration had negative effects on seedling establishment, while seed mass had a positive effect. A significant interaction between leaf litter input at a plot and seed size suggested that large seeded species had higher STS transition probability in plots with more leaf litter biomass. This effect was reversed for small seeded species. For lianas, leaf litter had a negative effect on STS transition and temporal fruiting concentration had a positive effect.

5. *Synthesis*. Our analyses demonstrate the multi-dimensional axes of regeneration niches and how they can be related to seed size. Long-term datasets are critical for understanding these relationships because the relevant factors vary along large spatial and temporal scales.

Key-words: life history trade-offs, Luquillo, plant population and community dynamics, Puerto Rico, regeneration niche, seed and seedling establishment limitation, successional niche

INTRODUCTION

The life cycle of plants is comprised of several remarkable transitions, during which individuals are culled from populations through a variety of mechanisms (Grubb 1977; Harper 1977; Schupp 1995). The seed to established seedling (STS) transition is one critical bottleneck in plant demography (Poorter 2007) with implications for community dynamics (Levine & Murrell 2003) and species relative abundances. Life history trade-offs (*i.e.* negative correlations between pairs of traits) that appear during the STS transition may be critical for creating and maintaining species diversity (Hubbell & Foster 1986; Pacala *et al.* 1996; Hubbell 2001).

A number of trade-offs may manifest during the STS transition. First, a negative relationship between competitive and colonization abilities (Levins & Culver 1971; Tilman 1994) can theoretically maintain diversity so long as a competitive dominance hierarchy is strictly maintained. This trade-off may appear during the STS transition as a result of differences in seed size among species, as small-seeded species are better colonizers (through higher fecundity or dispersal) and large seeded species are better competitors (Everham *et al.* 1996; Coomes & Grubb 2003). However, empirical support for strict dominance hierarchies is limited (Coomes & Grubb 2003). A second plausible trade-off may occur between fecundity and stress tolerance (Muller-Landau 2010); more fecund species persist by establishing in sites with favorable conditions simply by arriving first (colonization advantage). Less fecund but more stress tolerant species are able to establish in unfavorable conditions (*e.g.* drought or shade) despite being more seed limited throughout the landscape. Finally, species may inhabit specific successional niches (Pacala & Rees 1998), which involve trade-offs in the ability of species to survive at low resource conditions (*e.g.* shade) versus the ability to exploit the temporary resource-rich conditions generated in the wake of disturbance (*e.g.* fast growth in high light conditions). In the case of the STS transition, seedlings of early successional species may persist despite seed limitation because they are capable of high seedling establishment in recently disturbed sites (*e.g.* high light environments) (Dalling *et al.* 2004). Nevertheless, it is important to note that the trade-off in this model may be manifest at different life history stages (*e.g.* sapling or adult tree demography). Together, these three mechanisms illustrate how trade-offs between life-history traits may interact

105 with environmental heterogeneity to drive successional dynamics and maintain diversity
106 (Chesson 2000).

107 Conditions that mediate life history trade-offs during the STS transition can be
108 generally partitioned into those that limit dispersal (*i.e.* seed limitation) and those that
109 limit seedling establishment (*i.e.* safe-site limitation) (Turnbull *et al.* 2000; Muller-
110 Landau *et al.* 2002; Norden *et al.* 2009; Uriarte *et al.* 2010). Because seed arrival at a site
111 precedes seedling establishment, the importance of environmental heterogeneity in
112 governing species distributions may depend on the relative strength of seed versus
113 seedling establishment limitation. Seed limitation can result from either limited
114 production (low fecundity) or restricted dispersal of available seeds (Clark *et al.* 1998;
115 Terborgh *et al.* 2011). Following dispersal, seedling establishment can be limited by the
116 post-dispersal action of a wide variety of biotic and abiotic mechanisms (Muller-Landau
117 *et al.* 2002; Norden *et al.* 2007). Examining the relationship between seed and
118 establishment limitation, and how each relates to seed size, can shed light on the
119 processes governing the STS transition.

120 The particular mechanisms that regulate the STS transition involve a variety of
121 biotic factors such as seed predation, herbivory, and competition, all of which can be
122 exacerbated by high seed and seedling densities (Harms *et al.* 2000; Hille Ris Lambers *et*
123 *al.* 2002; Comita *et al.* 2009). In addition, abiotic factors, such as light availability and
124 leaf litter conditions interact with seed and seedling physiology and life history traits to
125 influence the likelihood that seeds germinate and become established seedlings in
126 heterogeneous environments (*e.g.* Pearson *et al.* 2002; Masaki *et al.* 2006; Norden *et al.*
127 2009).

Examining how trade-offs associated with dispersal and stress tolerance vary between life forms and successional stages may help determine how the processes that govern the STS transition differ among groups of ecologically similar species. Lianas (woody vines) and trees represent different life history strategies in tropical forests (Schnitzer & Bongers 2002). While previous studies comparing these groups have focused on the physiology of mature plants (Schnitzer 2005; Cai *et al.* 2009; DeWalt *et al.* 2010), a limited body of work suggests a similar growth/survival trade-off between life forms during early life stages (Gilbert *et al.* 2006; Cai *et al.* 2007). Despite the increasing attention given to liana dynamics in tropical forests (Schnitzer 2005; Schnitzer & Bongers 2011), we lack a detailed understanding of the dynamics of early life history stages that are critical in the maintenance of liana diversity. Another contrast exists between species associated with different successional stages. Pioneer species are typically associated with high fecundity, widespread dispersal and relative intolerance to environmental stress and limited resources. In contrast, late successional species tend to be less fecund and more robust to environmental stress and limited resources. As a result, species associated with different successional stages may display different responses to environmental heterogeneity.

Here, we employ seed rain and seedling establishment data collected over 3 years at the Luquillo Forest Dynamics Plot in Puerto Rico to explore how environmental heterogeneity and variation in life history characteristics (*e.g.* seed size, life form, successional association) influence the STS transition for 14 tree species (including 2 palms) and 5 liana species. We framed our study with two primary questions:

(1) Are there trade-offs in the strength of seed vs. seedling establishment limitation that are mediated by seed size? We predicted a trade-off between seed arrival and seedling establishment limitation, with larger seeded species being more seed limited (*i.e.* relatively low fecundity and dispersal, and greater predation) and smaller seeded species more limited by seedling establishment (*i.e.* relatively narrow regeneration niches and low competitive ability and stress tolerance).

(2) What are the biotic (*i.e.* seed size, life form, and con- and heterospecific seed density) and abiotic (*i.e.* light and leaf litter) factors that mediate the STS transition? If differences in seed size reflect a life-history trade-off relevant to the STS transition, we expected to find significant interactions between seed size and abiotic conditions. Specifically, we expected STS of small seeded species to be influenced positively by light (competitive ability) and negatively by leaf litter (stress tolerance) relative to large seeded species. We expected this prediction to vary across successional groups (*i.e.* small seeded pioneers versus relatively large seeded shade-tolerant species), and that trees and lianas would show similar patterns.

METHODS

Study Site. The Luquillo Forest Dynamics Plot (LFDP) is a 16-ha permanent plot (18°20'N, 65°49'W) in northeastern Puerto Rico. Classified as subtropical wet forest in the Holdridge life zone system (Ewel & Whitmore 1973), mean annual rainfall in the LFDP is 3,500 mm yr^{-1} and elevation ranges from 333 to 428 m a.s.l (Thompson *et al.* 2002). Soils are formed from volcaniclastic rock (Soil Survey Staff 1995). The LFDP has experienced a series of severe natural and human disturbances (Scatena & Larsen

1991; Thompson *et al.* 2002; Beard *et al.* 2005). Tropical storms have produced a highly dynamic community and some of the key processes that influence community composition have been identified (*e.g.* Uriarte *et al.* 2005; Uriarte *et al.* 2009). In addition, portions of the LFDP were used for agriculture and logging before 1934 (Thompson *et al.* 2002). As a result, the plot contains a mix of species representative of different successional stages and can be roughly divided into 'high' and 'low' sections of historic land-use intensity (Fig. S1; Uriarte *et al.* 2009).

Seed rain and seedling plots. Every two weeks, all fruits and seeds were collected from a network of 120 phenology baskets (Fig. S1; Zimmerman *et al.* 2007). These 0.5 m^2 baskets are constructed with 1 mm mesh mounted 1 m above the ground. Three 1 m^2 seedling plots are located 2 m away from each phenology basket (plot n=360). We refer to each phenology basket and its three associated seedling plots as a 'station'. Each year, all seedlings (all germinated woody stems < 1 cm diameter at 1.3 m (DBH)) are counted, tagged, and identified to species. Censuses took place between March 22 – April 20 in 2007, March 3 – April 11 in 2008, March 9 – June 18 in 2009 and March 5 – April 9 in 2010.

We applied the seed rain data from each phenology basket to each of the three associated seedling plots. As a result, the number of observed seedlings in a seedling plot sometimes exceeded the number of seeds counted in the corresponding phenology basket. Previous analyses (Hille Ris Lambers *et al.* 2002; Wright *et al.* 2005) addressed this issue by setting the number of seeds equal to seedling recruits for these observations. We followed this convention when calculating seed and seedling establishment limitation (see *Seed and seedling establishment limitation* below). This approach, however, results

196 in a mean per-seed STS transition probability (*i.e.* no. seedling recruits / no. seeds) equal
197 to one, artificially indicating 'ideal' conditions for establishment. Because this is both
198 biologically unrealistic and mathematically problematic for the models of the STS
199 transition we used, we introduced a conservative bias in our results by excluding these
200 observations from our model of STS transition described below (see Appendix 1 for
201 details about excluded observations).

202 *Species selection.* To ensure sufficient statistical power, we selected focal species
203 based on two criteria over the three years combined: (i) seeds (and seedlings) were
204 recorded from ≥ 10 baskets (and plots), and (ii) seed (and seedling) densities must have
205 varied by at least a factor of four among baskets (and plots). These criteria resulted in 19
206 focal species that represent a broad range of seed sizes, successional status, dispersal
207 modes, and evolutionary histories (Table 1). Fourteen of these species account for ~79%
208 of tree stems ≥ 10 cm DBH recorded live in the LFDP during the 2005 census. Although
209 lianas are not included in LFDP tree censuses, they are included in the seedling censuses.
210 In total, the 19 focal species account for > 95% of all seedlings recorded in each census
211 from 2008–2010.

212 *Seed and seedling establishment limitation.* In order to determine whether seed
213 size influenced the relative strength of seed and seedling establishment limitation for each
214 species (Question 1), we quantified the proportion of baskets not reached by seeds
215 ('fundamental seed limitation' sensu Muller-Landau *et al.* 2002) as:

216 $$\textit{Seed limitation}_i = 1 - \frac{a_i}{n} \qquad \text{[Eqn. 1]}$$

217 where a is the number of stations with seeds of species i, divided by the total number of
218 stations, n (here, n=120). The difference between seed limitation and new seedling

219 establishment provides an index of safe-site limitation ('realized establishment limitation'
220 sensu Muller-Landau *et al.* 2002), calculated as:

221 $$\textit{Seedling establishment limitation} = 1 - \frac{r_i}{6a_i} \quad \text{[Eqn. 2]}$$

222 where r is the number of seedling plots with seedling recruits of species i. We multiplied
223 a_i by 6 because seeds from each basket ($0.5m^2$) were used as an estimate of seed rain for
224 each of the 3 adjacent ($1m^2$) seedling plots. These calculations were based on the full
225 dataset of total seed rain and seedling establishment across all three study years. We used
226 a randomization procedure (see Appendix 2 for details) to determine if observed levels of
227 seed and seedling establishment limitation differed significantly from a null model in
228 which seeds and seedlings were Poisson distributed across stations (Norden *et al.* 2009).
229 The difference between the mean expected and observed seed limitation (δ_{Seed}) and
230 seedling establishment limitation ($\delta_{Establishment}$) ranges between -1 and 1; positive values
231 indicate higher limitation than expected, and vice versa. While these calculations assume
232 a uniform distribution of potential seed sources across the sample area, many species in
233 the LFDP are non-randomly associated with land-use history (Thompson *et al.* 2002;
234 Uriarte *et al.* 2009). As a result, we calculated δ_{Seed} and $\delta_{Establishment}$ separately for each of
235 the two main land-use portions of the LFDP and assessed the difference between these
236 categories for both δ_{Seed} and $\delta_{Establishment}$.

237 To determine mean per-seed success for each species, we calculated the total
238 number of established seedlings divided by six times the total number of seeds in the
239 phenology baskets recorded during the study (to standardize sampling effort). This
240 metric averages over environmental heterogeneity and provides a general picture of the
241 STS transition. Next, we discuss the data and methods used to explore the influence of

specific biotic and abiotic variables on STS transition in the LFDP.

Abiotic factors

Light. To measure light availability at each plot around the time of the seedling censuses we used hemispherical photography and an automated thresholding algorithm (Jonckheere *et al.* 2005) to calculate percent light transmission. Photographs were taken soon after dawn in uniform light conditions without direct sunlight or rain on the lens using a Sigma 4.5mm F2.8 EX DC fisheye lens mounted on a Nikon Coolpix camera and leveled at 1-m in the center of each plot. Percent light transmission calculated from photographs taken after each seedling census was used as a predictor variable for STS transition in the following year. Data are available upon request from the Luquillo LTER data repository (http://luq.lternet.edu/data).

Leaf litter. Leaf litter was collected in the phenology baskets every 2 weeks from August 2006–August 2007, oven dried at 70°C, and weighed. Here, we assumed that spatial variation among stations in leaf litter input remained constant over the three years of the study. This assumption is reasonable because (i) there were no large disturbances during this period and the climatic conditions remained relatively uniform, (ii) observations near the study site suggest that in the absence of severe disturbance, spatial variation in leaf litter exceeds temporal variation (D. Garcia-Montiel *unpublished data*), and (iii) our interest was in the impacts of relative spatial variation in leaf litter biomass, not absolute values. We calculated annual leaf litter input for each station (g m^{-2}) and applied this value to the associated plots for subsequent analyses.

Biotic factors

Temporal concentration of seed production. Fruiting phenology of our focal species differs dramatically, with some species being most productive within short periods and others producing more consistently through the year (Fig. S2; Zimmerman *et al.* 2007). We predicted that species that produce seeds in concentrated bursts would have lower STS than those with less temporally variable seed production because they might suffer more from negative density dependent factors (next section), and also that they might be exposed to sources of mortality for a longer time depending on the time between the fruiting peak and the subsequent seedling census. We might expect a high STS if a fruiting peak occurred shortly before a seedling census but given the phenology of our study species (Fig. S2) we expect this effect to be weak. We used the mean length of the fruiting vector calculated by Zimmerman *et al.* (2007) as a measure of temporal concentration of seed production.

Conspecific and heterospecific seed density. Negative density dependence factors (NDD) can influence the survival of tropical seedlings (Harms *et al.* 2000; Hille Ris Lambers *et al.* 2002; Comita *et al.* 2009) and may be a critical process driving observed species abundance patterns in the LFDP (Comita *et al.* 2010). To tease apart the effects of NDD from conspecific versus heterospecific seed density, we calculated the log (+1) transformed number of both conspecific and heterospecific seeds into each basket per year.

Seed size. We calculated species mean dry seed mass (g) by collecting and weighing 9─100 seeds per species (depending on abundance) from the Luquillo forest. Seed mass values were log-transformed prior to analyses because of the wide range of values among

288 our study species (Tables 1, S1).

289 *Statistical Analyses.* Since values of δ_{Seed} and $\delta_{Establishment}$ were approximately
290 normally distributed we used linear regression to examine the relationship between δ_{Seed}
291 and $\delta_{Establishment}$, as well as the relationship between each of these limitations and seed
292 mass (Question 1). We expected that a competition-colonization or fecundity-stress
293 trade-off would correspond to a negative correlation between δ_{Seed} and $\delta_{Establishment}$. If a
294 trade-off occurs in the ability of species to survive in low resource conditions (*e.g.* shade)
295 versus the ability to exploit the temporary resource-rich conditions generated in the wake
296 of disturbance as predicted by the successional niche model, uncovering the pattern may
297 hinge on the distribution of resources within the study area and time since disturbance.
298 To test this, we used ANOVA and *t*-tests to compare δ_{Seed} and $\delta_{Establishment}$ among species
299 of different successional groups (pioneer, secondary, late), life forms (trees and lianas),
300 and primary dispersal modes (animal vs. wind).

301 To evaluate specific factors associated with the STS transition (Question 2), we fit
302 statistical models where the response variable was the number of seedlings recruited in
303 individual seedling plots. The log of the number of seeds observed in each associated
304 nearby seed basket was included as an offset. Initial model residuals exhibited over-
305 dispersion so the results reported here are based on a generalized linear mixed model with
306 negative binomial errors. Abiotic covariates (light, leaf litter biomass), temporal fruiting
307 concentration, the logarithm of seed mass, and conspecific and heterospecific seed
308 density were included as fixed effects. Collinearity was less than 0.32 for all pairs of
309 predictor variables. We also included a random effect for seedling plots nested within a
310 single basket. To assess the evidence that the influence of abiotic factors on the STS

311 transition was mediated by seed size, we examined interaction terms between abiotic
312 factors and seed size in these models.
313 All continuous predictors were standardized prior to analyses by subtracting their
314 mean and dividing by twice their standard deviation (Gelman & Hill 2006). This
315 procedure enables a direct comparison of the magnitude and direction of covariate effects
316 based on their estimated coefficients in regression analyses (Schielzeth 2010).
317 Coefficients for all parameters were estimated using WinBugs (Spiegelhalter *et al.* 1999)
318 with weakly or non-informative priors, and models were judged to converge when R-hat
319 for all parameters were less than or equal to 1.1 (Gelman & Rubin 1992). We determined
320 statistical significance of predictor variables when 95% credible intervals did not overlap
321 with zero. We calculated multilevel goodness of fit (R^2) using methods derived from
322 Gelman and Pardoe (2006).
323
324 **RESULTS**
325 *Question 1: Are there seed-size mediated trade-offs in the strength of seed vs.*
326 *seedling establishment limitation?*
327 Although most species showed significant δ_{Seed} and $\delta_{Establishment}$ limitation, there
328 was considerable variation in the degree of seed and seedling establishment limitation
329 they displayed (Fig. 1, Table S2). In the low land-use portion of the plot δ_{Seed} and
330 $\delta_{Establishment}$ were positively correlated (P=0.032, Adjusted R^2=0.20) and not significantly
331 correlated in the high land-use portion of the plot (P=0.27). The positive correlation in
332 the low land-use portion of the plot disappeared when one outlying species, *Tabebuia*
333 *heterophylla*, was removed from the analysis. The relationship between $\delta_{Establishment}$ and

334 log seed mass was negative and significant in both the low (P=0.002, Adjusted R^2=0.42)
335 and high (P=0.02, Adjusted R^2=0.22) land-use portions of the plot (Fig. 2). The
336 relationship between δ_{Seed} and seed mass, however, was not significant in either land-use
337 portion of the plot (Fig. 2).

338 While species varied in the magnitude of δ_{Seed} and $\delta_{Establishment}$ between the two
339 land-use portions of the plot, most species exhibited consistent patterns in the sign of
340 each limitation regardless of land use. Across all species, the mean difference between
341 land-use categories for δ_{Seed} was 0.18 (+/- SD 0.15) and for $\delta_{Establishment}$ was 0.13 (+/- SD
342 0.10), indicating that both limitations are stronger in the high land-use portion of the plot
343 when averaged across species (Table 2). For most species, δ_{Seed} was significantly
344 positive in both land-use portions of the plot while $\delta_{Establishment}$ showed more mixed results
345 (Fig. 1 and Table S2).

346 We found some evidence for differences in $\delta_{Establishment}$ among successional groups
347 (Table S3). In the low land-use portion of the plot, successional group had a significant
348 effect on $\delta_{Establishment}$; pioneer species were more limited by seedling establishment
349 compared to late successional species (Tukey's HDS, P=0.03). Secondary forest species
350 had intermediate levels of $\delta_{Establishment}$ that were not significantly different from either
351 pioneer or late successional species. Successional group had no significant effect on δ_{Seed}
352 values in either land-use portion of the plot (Table S3).

353 Life form did not have a significant effect on either δ_{Seed} or $\delta_{Establishment}$; however,
354 lianas had significantly higher levels of per-seed success than trees (t = -5.7082 two-
355 tailed P<0.001; Fig. 3). For all species pooled or for lianas alone there was no significant
356 relationship between seed mass and per-seed success but when considering trees alone

357 there was a significant positive relationship (Fig. 3; P=0.046, Adjusted R^2=0.23). This
358 relationship became stronger when two outliers (*Prestoea montana* and *Guarea guidonia*)
359 were removed (P<0.001, Adjusted R^2=0.68). Primary dispersal mode (animal vs. wind)
360 was not related to either δ_{Seed} or $\delta_{Establishment}$ (Table S3).
361
362 *Question 2: What biotic and abiotic factors mediate the STS transition?*
363 Several abiotic and biotic factors had significant effects on the probability of STS
364 transition (Fig. 4). In the full model, life form had the strongest effect on STS with lianas
365 having significantly greater STS transition probability than trees. Goodness of fit for the
366 data model was R^2=0.20. We subsequently ran separate models for each life form to
367 explore this variation. While light conditions did not have a significant direct effect on
368 the STS transition for either life form, leaf litter biomass had a significantly negative
369 effect for lianas. Mean fruiting vector was positively associated with the STS transition
370 for lianas but negatively so for trees. Seed mass was positively associated with the STS
371 transition for both life forms but only significantly for trees. Heterospecific seed density
372 did not have a significant effect on the STS transition for either life form. Conspecific
373 seed density had a significant negative effect on the STS transition for trees but not
374 lianas.
375 We expected significant interactions between abiotic covariates and seed size to
376 reveal a role of environmental factors in mediating the STS transition depending on seed
377 size. We detected only one significant interaction between leaf litter biomass and seed
378 size for trees but not lianas (Fig. 4). Small-seeded tree species had reduced STS in plots

379 with higher levels of leaf litter biomass while large-seeded species had slightly increased
380 STS in plots with higher levels of leaf litter biomass.
381
382 **DISCUSSION**
383 Considerable attention has been given to establishing the importance of life
384 history trade-offs in the maintenance of diversity in natural communities (Levins &
385 Culver 1971; Pacala & Rees 1998). Trade-offs associated with seed size diversity have
386 been of particular interest (Coomes & Grubb 2003; Moles & Westoby 2006; Muller-
387 Landau 2010). Here we paired hypotheses about life history trade-offs with analyses of
388 potential biotic and abiotic factors that might mediate them in natural systems. We
389 discuss our results in the context of the maintenance of diversity in tropical forests.
390
391 ***Question 1:*** *Are there trade-offs in the strength of seed vs. seedling establishment*
392 *limitation?*
393 Nearly all species examined here displayed strong seed limitation. By controlling
394 for 'source limitation' (no. of seeds), our null model tested for significant 'dispersal'
395 limitation (sensu Muller-Landau *et al.* 2002). Therefore, if observed seed limitation
396 differed by land use history and δ_{Seed} did not, then we could conclude that observed seed
397 limitation was due to source limitation (few or low fecundity adult trees) and not
398 dispersal limitation. However, we did not find evidence for this relationship between
399 land-use areas by successional group. Therefore, despite the observed relationships
400 between mature tree abundances and land use history in the LFDP (Thompson *et al.*

401 2002), our results are inconclusive about how seed limitation specifically contributes to
402 differences in community composition across the LFDP.
403 We explicitly looked for a negative correlation between δ seed limitation and δ
404 establishment limitation with the expectation that if a competition-colonization or
405 fecundity-stress trade-off were operating, we would detect a negative correlation between
406 these limitations. In fact, we found a positive correlation in the low intensity land-use
407 portion of the plot. However, this unexpected relationship was largely dependent on one
408 outlier species.
409 The relationship between δ_{Seed} and seed mass, predicted to be negative by the
410 competition/colonization trade-off (Tilman 1994; Coomes & Grubb 2003), was not
411 significant. One relatively large-seeded species (*P. montana*) accounted for 50% of
412 stems ≥10cm DBH in the 2005 tree census, and its dominance may have inflated
413 measures of STS transition by overwhelming seed input. However, seed size was
414 negatively related to $\delta_{Establishment}$, as expected if trade-offs are mediated by seed-size
415 dependent stress tolerance (Muller-Landau 2010). The positive association between seed
416 mass and per-seed success for trees also suggests a germination advantage for large
417 seeded species. These results conform with those of an experimental germination study
418 of 119 Puerto Rican tree species (Francis & Rodriguez 1993), which found a positive
419 relationship between seed mass and percent of seeds germinating across a broad range of
420 seed mass values ($1.6x10^{-5}$ to 71g). These results provide some support for a
421 competition-colonization or fecundity-stress tolerance trade-off related to seed size
422 (Tilman 1994; Coomes & Grubb 2003; Muller-Landau 2010), but demonstrate how large
423 seeded species (*i.e. P. montana*) can overcome seed limitation if they are very common

as reproductive adults. A second species, *G. guidonia*, accounted for <2% of stems ≥10cm DBH in the 2005 tree census and its relatively high STS transition probability is more difficult to explain. One possibility is that *G. guidonia* experiences a recruitment bottleneck after the STS transition (Fernandez del Viso 1997).

We also found some evidence supporting the successional niche hypothesis. After controlling for variation in seed source abundance across land use portions in the plot, pioneer species had higher seedling establishment limitation compared with late successional species in the low land-use intensity portion of the plot, indicating that successional groups may have differential seedling establishment success depending on land use history (Comita *et al.* 2010).

Question 2: What biotic and abiotic factors mediate the STS transition?

Biotic drivers

Together with the observed negative relationship between seed mass and $\delta_{Establishment}$, the positive effect of seed mass on STS transition for trees supports the notion that large seed size conveys tolerance to stress or competitive advantage. The most striking difference in STS transition probability in our analysis, however, was between lianas and trees. In this study, lianas had much higher STS transition probabilities than expected given their seed sizes. In addition, seedling establishment limitation was generally lower for lianas than trees despite spanning nearly the same range of seed limitation. Our results suggest a potential for differences among life forms in terms of their regeneration niches.

One possible explanation for our findings is that lianas face more intense filtering

447 in life stages beyond the STS transition. Unlike freestanding trees, lianas require
448 auxiliary vertical support structures to facilitate their growth into the forest canopy
449 (Schnitzer & Bongers 2002). It is feasible that this precarious lifestyle may impose
450 higher selective pressure to succeed during the STS transition in order to increase the
451 chance of establishing near a suitable support structure. Differences among species in
452 terms of their seedling functional morphology (Garwood 1996; Ibarra-Manríquez *et al.*
453 2001; Baraloto & Forget 2007) provide another possible explanation for our results. All
454 species included in our study belong to two functional morphology types: cryptocotylar
455 epigeal reserve (CER) and phanerocotylar epigeal foliar (PEF) *sensu* Garwood 1996. All
456 of the lianas belong to the CER-type while all of the pioneer tree species belong to the
457 PEF-type (C.N., *personal observations*). CER species tend to have relatively low relative
458 growth rates and larger seeds than the PEF species (Ibarra-Manríquez *et al.* 2001;
459 Baraloto & Forget 2007).
460 We expected temporal concentration of seed production to be negatively related
461 with STS transition because of increased strength of NDD effects, and longer exposure to
462 mortality hazards prior to seedling censuses. Instead, we found contrasting responses
463 between lianas (positive) and trees (negative). Thus, temporal concentration of seed rain
464 suggested an effect of NDD in trees (see below) but not in lianas. The timing of seed
465 production relative to the seedling censuses could account for this difference (*i.e.* if lianas
466 and trees tended to produce most seeds shortly before and after seedling censuses,
467 respectively). However, the timing of seed production was not consistent across years
468 and some abundant trees also exhibited fruiting peaks shortly before census periods (*e.g.*
469 *Dacryodes excelsa*, *Ocotea leucoxylon*). We conclude that the observed differences

between life forms are unlikely to be fully explained by phenological differences in seed production.

We found a negative effect of conspecific seed density on STS transition probability for trees. Intraspecific seed density has previously been shown to have negative effects on seedling survival in the LFDP (Comita *et al.* 2009) and in other forested systems (Harms *et al.* 2000; Hille Ris Lambers *et al.* 2002). For tropical tree seedlings, mechanisms of negative density dependence other than competitive effects (*i.e.* Janzen-Connell effects) are probably most important (Paine *et al.* 2008). Neither conspecific nor heterospecific seed density had a significant effect on STS transition for lianas.

Abiotic drivers

Consistent with numerous other studies that have demonstrated strong effects of leaf litter on seedling emergence (*e.g.* Guzman-Grajales & Walker 1991; Everham *et al.* 1996; Sayer 2006; Dupuy & Chazdon 2008), we found a significant negative effect of leaf litter biomass on STS transition that was significant for lianas. The lack of a significant effect for trees may indicate that our leaf litter biomass data do not accurately capture among year variation in leaf litter input to seedling plots. Another possible explanation for the lack of a direct effect on trees is that species differ in their response to leaf litter conditions. In fact, we found a significant interaction between leaf litter biomass and seed size, which we discuss in the following section.

We expected light to have a positive direct effect on STS transition because it is an essential resource for plants and can also act as a germination cue (Swaine &

493 Whitmore 1988; Vazquez-Yanes *et al.* 1990). Contrary to this expectation, we found no
494 direct effect of light on STS transition for either life form. An interactive effect between
495 light and leaf litter conditions could obscure this relationship. It is also possible that high
496 seed or seedling mortality in plots with very high light levels (*i.e.* canopy gaps)
497 contributed to this result through desiccation. However, in their community-level
498 analysis in the LFDP, Comita *et al.* (2009) found a positive effect of light on seedling
499 survival only shortly after a hurricane, where the degree of canopy openness was
500 substantially higher than the levels recorded in this study. After the canopy closed (*i.e.* 4-
501 6 years following a major hurricane), factors other than light (*e.g.* conspecific seedling
502 density, seedling height) were likely more important drivers of seedling survival.
503 We hypothesized that larger seeded species would have higher overall STS
504 transition rates but abiotic conditions would interact with this trait to modulate the STS
505 transition (Moles & Westoby 2006). Specifically, we expected that STS transition of
506 small seeded species would be influenced positively by light and negatively by leaf litter
507 relative to large seeded species. Concordantly, we found a significant interaction
508 between seed size and leaf litter biomass on STS transition probability for trees. Large
509 seeded tree species exhibited higher STS probabilities in plots with high leaf litter
510 biomass, possibly reflecting lower seed predation or reduced desiccation (Sayer 2006).
511 In contrast, high levels of leaf litter biomass reduced STS transition probability for small
512 seeded species that might have been buried without the resources to successfully
513 germinate, root or reach a higher light environment (*e.g.* Sayer 2006; Dupuy & Chazdon
514 2008). Previous research in the Luquillo forest found a negative effect of leaf litter for
515 four species, including the large-seeded tree, *Dacryodes excelsa* Vahl (Guzman-Grajales

& Walker 1991). Guzman-Grajales & Walker (1991) mimicked litter inputs immediately following a major hurricane (Hugo), which exceeded the total annual litter input during baseline years (Lodge *et al.* 1991). Our study represents variation in litter input over a "normal" year as opposed to a single experimental simulation of a severe disturbance.

We found no evidence of an interaction between light conditions and seed size on the STS transition. The smallest seeded species in our study were the pioneers (*Cecropia schreberiana*, *Schefflera morototoni*, and *Alchorneopsis floribunda*), all of which are categorized as 'high light regenerators' (Devoe 1989). The relatively large seeded, late successional trees included in this study are considered shade-tolerant and their seedlings can survive for long periods in closed canopy forests (Devoe 1989). Leishman & Westoby (1994) found that large seeds enjoy an advantage over small seeds most evident in extreme shade conditions (95-99%) because of larger initial energy reserves and higher growth rates. It is possible that relative small range of light levels throughout the plot were not sufficient to reveal differential responses of individual species.

Despite the extensive body of research on the ecological and evolutionary consequences of interspecific variation in seed size, the germination and establishment biology of lianas, in our study site and elsewhere, remain understudied. Additional research should examine variation among life forms in germination success and the conditions influencing germination of lianas. It is possible that we did not find evidence of interactions between seed size and environmental conditions for this group because the range of seed size for the lianas in this study was relatively narrow (compared to trees) even though seed size of the 5 lianas included here spanned 2 orders of magnitude (0.051-0.395 g).

539

540 *Conclusions*

541 Exploring the ecological correlates of variation in seed size has received a
542 tremendous amount of theoretical and empirical attention. This is because seed size is
543 assumed to modulate critical ecological processes (*i.e.* fecundity, dispersal, competitive
544 ability and stress tolerance) relevant to community dynamics and the maintenance of
545 species diversity (Coomes & Grubb 2003; Muller-Landau 2010). Our results from the
546 LFDP support the role of seed size in modulating some aspects of the STS transition in
547 tropical forests. Seed size alone, however, may not capture many differences among
548 species in their response to the environmental conditions that limit establishment,
549 particularly in cross-site comparisons.

550 Some caveats to our results bear discussion. Firstly, seed production in tropical
551 forests can vary substantially across years (Norden *et al.* 2007) and the effects of NDD
552 can vary depending on the overall seed production (Wright *et al.* 2005). Because the
553 dataset analysed for this study spans only three years, we are unable to rigorously explore
554 temporal variability in seed rain or the STS transition. Additionally, variation among
555 species in their ability to persist in the seed bank likely contributes to variation in
556 observed STS transition (Dalling *et al.* 2011). Second, Puerto Rico lacks a large native
557 vertebrate fauna that, in other tropical forests, can play a key role in seed dispersal and
558 seed predation. Additionally, particular disturbance regimes are likely to influence
559 species composition in complex ways that cannot be fully captured by one study.
560 Additional information on various biotic hazards governing the STS transition including
561 post-dispersal seed predation, pathogen attack, and seedling herbivory could provide

562 valuable insight. These processes are variable in time and space and their roles in early
563 life stage transitions of plants remain to be synthesized in terms of life history trade-offs.
564 Fortunately, long-term datasets appropriate for addressing these issues are becoming
565 increasingly available (*e.g.* through the Center for Tropical Forest Science [CTFS]
566 network). Our study demonstrates the utility of using long-term field data to address
567 fundamental questions about life history trade-offs in plant communities.
568

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581

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix 1. *Details of excluded observations.*
Appendix 2. *Null model of seed and seedling limitation.*
Table S1. *Explanatory variables used in the various models with observed ranges.*
Table S2. *Observed and randomized seed limitation and seedling establishment limitation for 19 species in the LFDP.*
Table S3. *Summary statistics for ANOVA's.*
Figure S1. *The Luquillo Forest Dynamics Plot and seed trap locations.*
Figure S2. *Cumulative proportion of total seeds collected from each of the 19 focal species and the grand total between August 2006 and May 2010.*

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794 **Table 1.** Characteristics of focal species

Code	Species	Family	Life form	Successional group[1]	Seed mass[2] (g)	Total observed seeds	Total observed recruits	Mean per seed success[3]	Primary dispersal vector[5]
AF	*Alchorneopsis floribunda* (Benth.) Muell. Arg.	Euphorbiaceae	Tree	Pioneer	0.007	16,455	11	0.003	A
CS	*Cecropia schreberiana* Miq.	Urticaceae	Tree	Pioneer	0.001	369,755	70	0.000	A
CD	*Chionanthus domingensis* Lam.	Oleaceae	Tree	Secondary	0.54	132	21	0.047	A
DE	*Dacryodes excelsa* Vahl	Burseraceae	Tree	Late	1.255	4,583	665	0.074	A
DG	*Drypetes glauca* Vahl	Putranjivaceae	Tree	Late	0.365	101	21	0.087	A
GG	*Guarea guidonia* (L.) Sleumer	Meliaceae	Tree	Secondary	0.251	682	398	0.219	A
HL	*Heteropteris laurifolia* (L.) A. Juss.	Malpighiaceae	Liana	-	0.072	1,007	707	0.215	W
HV	*Hippocratea volubilis* (L.)	Celastraceae	Liana	-	0.1	3,258	2,107	0.289	W
MB	*Manilkara bidentata* (A. DC.) A. Chev.	Sapotaceae	Tree	Late	0.594	278	39	0.044	A
MD	*Matayba domingensis* (DC.) Radlk.	Sapindaceae	Tree	Late	0.161	580	68	0.059	A
OL	*Ocotea leucoxylon* (Sw.) Laness	Lauraceae	Tree	Secondary	0.177	204	22	0.045	A
PP	*Paullinia pinnata* (L.)	Sapindaceae	Liana	-	0.395	205	109	0.186	A
PM	*Prestoea montana* (R. Graham) G. Nicholson	Arecaceae	Palm	Secondary	0.733	14,074	4,046	0.158	A
RS	*Rourea surinamensis* Miq.	Connaraceae	Liana	-	0.145	9,484	4,479	0.190	A
RB	*Roystonea borinquena* O.F. Cook	Arecaceae	Palm	Secondary	0.309	779	121	0.071	A
SM	*Schefflera morototoni* (Aubl.) Decne. & Planch.	Araliaceae	Tree	Pioneer	0.001	12,024	190	0.025	A
SV	*Securidaca virgata* (Sw.)	Polygalaceae	Liana	-	0.051	824	445	0.180	W
TH	*Tabebuia heterophylla* (DC.) Britton	Bignoniaceae	Tree	Secondary	0.011	5,062	281	0.027	W
TB	*Tetragastris balsamifera* (Sw.) Kuntze	Burseraceae	Tree	Late	1.14	444	47	0.064	A

795

[1] Successional group is based on information from Devoe (1989); [2] Dry seed mass (g); [3] Mean per seed success is calculated as the number of recruits divided by seeds (with the observed number of seeds from a trap applied to each of three associated seedling plots); [4] Dispersal mode follows Devoe (1989) and Uriarte *et al.* (2005): A=animal, W=wind.

Table 2. The difference between observed seed and seedling establishment limitation in the low and high land-use intensity portions of the LFDP. Positive values indicate that the species was more strongly limited in the high land-use intensity relative to the low land-use intensity portions of the plot

Species	Land-use difference: Seed Limitation	Land-use difference: Seedling Establishment Limitation
AF	0.22	-0.03
CS	0.00	-0.14
CD	0.14	0.04
DE	0.10	0.26
DG	0.31	-0.02
GG	0.14	-0.02
HL	0.25	0.19
HV	0.37	0.27
MB	0.30	0.09
MD	0.42	0.06
OL	0.02	-0.10
PP	0.02	-0.08
PM	0.00	-0.05
RS	0.00	0.15
RB	0.02	0.11
SM	-0.05	-0.16
SV	-0.37	0.13
TH	-0.31	-0.31
TB	0.36	0.36

FIGURE LEGENDS

Fig 1. Difference between observed and randomized seed and seedling establishment limitation (δ_{Seed} and $\delta_{Establishment}$) for 19 species in the low (A) and high (B) land-use intensity portions of the LFDP (see Table 1 for species codes). Positive values indicate higher limitation than expected by random and vice-versa. Error bars represent 95% confidence intervals (see Table S2 for more details). Note that some error bars are too small to visualize.

Fig 2. Log-transformed seed mass (g) versus δ_{Seed} (A, B) and $\delta_{Establishment}$ (C, D) for the low (A, C) and high (B, D) land-use intensity portions of the LFDP. See Table 1 for species codes.

Fig 3. Log-transformed seed mass and mean per-seed success for 19 focal species across all seedling plots and all 3 years (see Table 1 for species codes).

Fig 4. Mean standardized coefficients and 2.5% and 97.5% credible intervals of the effects of abiotic and biotic covariates on STS transition probability in the LFDP. The response variable was the number of seedlings recruited in individual plots (see Methods: Statistical Analyses). These results are based on negative binomial generalized linear mixed models with a log link. Filled circles indicate significant effects (*i.e.* credible intervals do not overlap zero).